How does habitat filtering affect the detection of conspecific and phylogenetic density dependence?

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How does habitat filtering affect the detection of conspecific and phylogenetic density dependence?

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Abstract

Conspecific negative density-dependence (CNDD) has been recognized as a key mechanism underlying species coexistence, especially in tropical forests. Recently, some studies have reported that seedling survival is also negatively correlated with the phylogenetic relatedness between neighbors and focal individuals - termed phylogenetic negative density-dependence (PNDD). In contrast to CNDD or PNDD, shared habitat requirements between closely related individuals are thought to be a cause of observed positive effects of closely related neighbors, which may affect the strength and detectability of CNDD or PNDD. In order to investigate the relative importance of these mechanisms for tropical tree seedling survival, we used generalized linear mixed models to analyze how the survival of more than 10,000 seedlings of woody plant species related to neighborhood and habitat variables in a tropical rainforest in southwest China. By comparing models with and without habitat variables, we tested how habitat filtering affected the detection of CNDD and PNDD. The best-fitting model suggested that CNDD and habitat filtering played key roles in seedling survival, but that, contrary to our expectations, phylogenetic positive density-dependence (PPDD) had a distinct and important effect. While habitat filtering affected the detection of CNDD by decreasing its apparent strength, it did not explain the positive effects of closely-related neighbors. Our results demonstrate that a failure to control for habitat variables and phylogenetic relationships may obscure the importance of conspecific and heterospecific neighbor densities for seedling survival.

Key words: *competition, habitat association, Janzen-Connell hypothesis, mixed models, phylogenetic relatedness, tropical forest*

INTRODUCTION

Tree populations are often thought to be regulated by negative density dependence (NDD), thereby making NDD an important mechanism underlying the maintenance of species diversity across multiple life stages (e.g., Wills et al. 1997, Harms et al. 2000, Peters 2003, Volkov et al. 2005, Comita et al. 2010, Swamy et al. 2011, Johnson et al. 2012, Comita et al. 2014). Intraspecific competition and Janzen-Connell effects (Janzen 1970; Connell 1971) via species-specific natural enemies (seed predators, pathogens and herbivores) are two main drivers of NDD (Wright 2002). Many studies have tried to demonstrate NDD by examining the relationship between plant survival, recruitment or growth and the densities of conspecific neighbors. Such studies, typically conducted using seedlings, have frequently found conspecific negative density dependence (CNDD) in the species studied (e.g., Webb and Peart 1999, Comita et al. 2010, Chen et al. 2010, Lin et al. 2012, Johnson et al. 2012).

The effects of intra- and inter-specific density on seedlings may be interchangeable if pathogens have wide host ranges where neighborhood density *per se* drives NDD and it is not necessary to invoke CNDD (Freckleton and Lewis 2006). However, tropical forest investigations that have partitioned their analyses into conspecific and heterospecific effects have often found significant differences in intra- and inter-specific effects (e.g., Peters 2003, Comita and Hubbell 2009, Johnson et al. 2012, Lin et al. 2012). This has supported the widespread view that seedling performance is limited more by interactions with conspecific individuals than heterospecific individuals. If generally valid, the greater strength of negative intra-specific effects relative to negative inter-specific effects (i.e., niche differences) promotes stable species coexistence (Chesson 2000).

Interestingly, conspecific adult neighbor densities have been found to have a particularly

63 strong negative influence on seedling survival (e.g., Comita and Hubbell 2009, Chen et al. 2010,
64 Johnson et al. 2014). Seedling-seedling interactions, in contrast, are often relatively weak,
65 presumably because the sizes and densities of seedlings in the understory of tropical forests are
66 not typically great enough to generate such large impacts (Paine et al. 2008, Svenning et al.
67 2008). Further, positive correlations between the probability of seedling survival and
68 heterospecific neighbor densities have been found (Comita and Hubbell 2009), supporting the
69 so-called 'species herd protection hypothesis' (Peters 2003). Thus, seedling survival is likely to
70 be lower in an area of high conspecific adult neighbor density and higher in an area with many
71 heterospecific adult neighbors.

72 Due to the enormous diversity in the tropics, heterospecific neighbors are more common
73 than conspecific neighbors. A simple division of neighbors into conspecifics and heterospecifics
74 may therefore hide the potentially large variation in the degree to which heterospecific species
75 are similar to the focal species. Such thinking led Webb et al. (2006) to characterize
76 heterospecific species in terms of their phylogenetic distance from the focal individual, thereby
77 moving neighborhood analyses beyond a potentially overly-simplistic conspecific/heterospecific
78 dichotomy.

79 The rationale for considering phylogenetic relatedness in studies of NDD rests on empirical
80 evidence suggesting that there is often a phylogenetic signal in morphological and biochemical
81 traits that dictate host-pest interactions (Mitter et al. 1991). In the most extensive syntheses to
82 date, the probability of sharing a pest or pathogen between two host plants decays strongly with
83 phylogenetic distance (Parker and Gilbert 2004, Novotny et al. 2006, Gilbert and Webb 2007,
84 Gilbert et al. 2012). This pattern is expected to be more pronounced under broader taxonomic
85 samples, and less pronounced under smaller taxonomic samples (e.g., a single genus).

Phylogenetic negative density dependence, due to shared natural enemies between closely related species, may therefore be expected to emerge in a tropical forest containing many plant lineages (i.e., a broad taxonomic sample). In such cases, CNDD can be extended across evolutionary distance between two neighboring species (e.g., Webb et al. 2006, Metz et al. 2010, Liu et al. 2012, Paine et al. 2012, Lebrija-Trejos et al. 2014) therefore generating phylogenetic negative density dependence (PNDD).

Beyond biotic interactions, an important driver of local community composition is the abiotic environment (Metz et al. 2010). For example, variation in light availability (Comita et al. 2009, Queenborough et al. 2009, Rüger et al. 2009), soil water availability (Comita and Engelbrecht 2009, Lin et al. 2012) and soil nutrients (Bai et al. 2012) are all well-known drivers of species survival, coexistence and diversity.

Findings that survival probability is positively correlated with conspecific density are often interpreted as being due to species' habitat preferences (e.g., Comita et al. 2009, Comita and Hubbell 2009, Lin et al. 2012). Indeed, many studies examine species' habitat preferences by analyzing the association between species occurrence and habitat variables (e.g., topography, light, soil nutrients, water availability etc.) at the seedling stage (e.g., Webb and Peart 2000, John et al. 2007, Comita et al. 2007, Comita and Engelbrecht 2009, Metz 2012). However, we argue that such results do not necessarily indicate a lack of biotic interactions in general or NDD in particular. Specifically, biotic interactions are dictated by the abiotic context, and a shared habitat preference does not negate the possibility of NDD. Rather, it is likely that habitat preferences and NDD operate simultaneously to produce observed species composition and population dynamics (e.g., Comita et al. 2009, Chen et al. 2010, Bai et al. 2012, Piao et al. 2013). In order to elucidate such a scenario, nested models that consider density effects without and with the abiotic context

are needed.

In this study, we used a population dynamics dataset of 10,316 seedlings for 269 woody plant species for four contiguous one-year census intervals in the 20-ha Xishuangbanna tropical seasonal rainforest dynamics plot in southwest China. Using generalized linear mixed models, we explored the relative importance of CNDD, PNDD and habitat filtering for seedling survival. Specifically, we built models of seedling survival dependent on the densities of conspecific and heterospecific neighbors and on the phylogenetic dissimilarities between heterospecific neighbors and focal seedlings. Each of these models was built without and with habitat variables to determine the degree to which habitat filtering affected the apparent prevalence of NDD. We specifically ask: (*i*) Does scaling the effects of neighbors by their phylogenetic distances improve model fit?; (*ii*) What is the relative importance of CNDD, PNDD and habitat filtering in our study system?; and (*iii*) How does habitat filtering affect the detectability of CNDD and PNDD?

METHODS

Study site

The study was conducted within the 20-ha Xishuangbanna Forest Dynamics Plot (XSBN), located in Mengla, Yunnan Province, Southwestern China (101°34′ E, 21°36′ N). The elevational range of the plot is from 709 m above sea level (asl) to 869 m asl (Lan et al. 2012) (Fig. S1). There is a rainy season from May to October and a dry season from November to April in the following year. Mean annual precipitation is approximately 1500 mm, of which 80% occurs from May to October (Cao et al. 2006).

The XSBN plot (400×500 m) was established in 2007 and censuses are carried out every 5 years. All woody stems with a diameter at breast height (DBH) ≥ 1 cm are tagged, identified,

132 measured and mapped (See detailed methods in Condit 1998). A detailed description of the
133 climate, geology and flora of XSBN can be found in Cao et al. (2008).
134
135 Seedling quadrats
136 During March 2010, a total of 500 seedling quadrats (2×2 m) were established in a regular
137 pattern in the center of each 20×20 m subplot in the 20-ha XSBN plot. Where obstacles such as
138 streams, large trees, rocks or fallen woods prevented the establishment of seedling quadrats in
139 these locations, they were placed instead in nearby 5 × 5 m subplots. In each of the 500 seedling
140 quadrats, all woody (tree, shrub and liana) seedlings with DBH < 1 cm and height ≥ 20 cm were
141 tagged, identified to species and measured for height. In this study, we used seedlings with height
142 ≥ 20 cm as focal seedlings because seedlings with this height can be assumed to be established in
143 our study system, and therefore more likely to be dependent upon relevant biotic and abiotic
144 interactions rather than effects of chance events that drive mortality in younger seedlings.
145 Seedling quadrats were subsequently censused in the late dry season (April and May) 2010,
146 2011, 2012, 2013 and 2014. In each census, the states (alive or dead) of all the woody seedlings
147 alive at the previous census were recorded and all new recruits to the 20-cm height threshold
148 were identified and tagged.
149
150 Neighborhood variables
151 At the first (2010) census, we defined total seedling neighbor density of each seedling quadrat as
152 the number of seedlings within the quadrat. Conspecific and heterospecific seedling neighbor
153 densities were defined in the same way. At subsequent censuses, we recalculated seedling
154 neighbor densities by excluding dead seedlings and adding newly recruited seedlings. Tree, shrub

and liana seedlings were monitored at the censuses, and all were included in the calculation of heterospecific seedling neighbor densities, although lianas were not included as focal seedlings in our models. Seedlings that were impossible to classify by species (121 in the 2010 census) were included in heterospecific neighbor counts, but not as focal seedlings.

We calculated the total adult neighbor density (TA) as the summed basal area (BA) of nearby adults weighted by their distances to the focal seedling (Canham et al. 2004):

$$\mathrm{TA} = \sum_{i}^{N} \frac{\mathrm{BA}_i}{\mathrm{Distance}_i}$$

where *N* is the number of adult neighbors. Conspecific and heterospecific adult neighbor densities were calculated in the same way. Models with densities calculated over a distance of 20 m had stronger support than those with densities calculated over distances of 10 m or 30 m (Table S1). In the following analyses, we therefore used total, conspecific and heterospecific adult neighbor densities calculated over 20 m. As a result, data from 86 of the 500 seedling quadrats were excluded from the following analyses because these quadrats were within 20 m of the edge of the XSBN plot, and therefore had incomplete adult neighbor density values.

Construction of phylogenetic tree and indices of phylogenetic dissimilarity

We have previously produced a molecular phylogeny for 428 species in the 20-ha XSBN plot (Yang et al. 2014). A total of 121 species identified in the 20-ha plot and/or the seedling quadrats were added to this phylogeny using the APE package (Paradis 2006) in R software (v. 3.0.2) (R Development Core Team 2014). These species were added at the crown node of the most closely related taxonomic level (genus, family or order) in the original molecular phylogeny. For example, any species missing from the original phylogeny that had a congener in the original

177 phylogeny was manually added to the phylogeny at the node for that genus. If there was no
178 congener in the original phylogeny, then the species was added to the node for its family in the
179 original phylogeny. A total of 18 species could not be added to the phylogeny because they were
180 from orders not in the original phylogeny. These species only constituted < 1 % of all individuals
181 in the seedling quadrats and therefore had little influence on our results.
182 Four phylogenetic diversity indices quantifying phylogenetic dissimilarity between focal
183 seedlings and their heterospecific neighbors were used in our analyses: total phylogenetic
184 diversity (TOTPd), average phylogenetic diversity (AVEPd), relative average phylogenetic
185 diversity (APd') and relative nearest taxon phylogenetic diversity (NTPd'). The TOTPd and
186 AVEPd are, respectively, the sum and average of the phylogenetic distances between a focal
187 seedling and its heterospecific neighbors. The APd' and NTPd' (proposed by Webb et al. 2006)
188 respectively quantify the deviation of observed average phylogenetic distance between a focal
189 seedling and its heterospecific neighbors from that expected under a null model, and the
190 equivalent deviation of observed phylogenetic distance between a focal seedling and its most
191 closely-related heterospecific neighbor. The null model used in this study shuffled the names of
192 species on the phylogeny 999 times to produce a null distribution of neighborhood phylogenetic
193 diversities. Positive APd' and NTPd' indicate that neighbors are less related to the focal seedling
194 than expected under the null model and negative APd' and NTPd' indicate that the neighbors are
195 more related than expected. We recalculated the four phylogenetic diversity indices at each
196 census after 2010 to exclude dead seedlings and add newly recruited seedlings. The indices were
197 calculated separately for heterospecific seedling neighbors and heterospecific adult neighbors
198 (with the adult neighborhood again defined as having a radius of 20 m).
199

Habitat variables

Habitat variables for each of the 414 target seedling quadrats were characterized using measurements of canopy openness, soil properties and topography.

Canopy openness: For each seedling quadrat, hemispherical photographs were used to obtain a measure of canopy openness (Comita et al. 2009, Queenborough et al. 2009), which indicated the light condition in the understory. Hemispherical photographs was taken 1.3 m above-ground at the center of each quadrat, using a Nikon Coolpix 4500 camera equipped with a Nikon FC-E8 Fisheye Converter lens in January 2014. The camera was arranged horizontally with the aid of a spirit level and pointed to the geographic south. Black and white JPG-images of 2272×1704 pixels were produced in accordance with the methods of Queenborough et al. (2009). The 'high contrast' setting increased distinction between sky and foliage. Three to five replicate photos were taken using a fixed aperture of f/7.5 and shutter speeds between 1/1000 and 1/30 s. Photographs were taken in uniformly overcast weather, during either early dawn or late dusk. The photograph showing the highest contrast between sky and foliage for each quadrat was selected. Gap Light Analyser software (GLA, version 2.0) was used to convert photographs to a single canopy openness measure following the protocol of Beaudet and Messier (2002).

Soil properties: Soils were sampled following the protocol of John et al. (2007). The 20-ha plot was divided into regular grid squares of 30×30 m, and two soil samples were taken at depths of 10 cm (without litter and humus) and random distance combinations of 2 m and 5 m, 2 m and 15 m, or 5 m and 15 m in a random direction from the grid point. A total of 765 soil samples were obtained. Soil pH, organic matter content (C), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available nitrogen (AN), available phosphorus (AP), available potassium (AK) and soil bulk density within each sample were measured (for details see Hu et al. 2012).

We used the residuals from polynomial trend-surface regressions for these soil variables to compute empirical variograms, to which we fitted variogram models and used ordinary kriging to obtain spatial predictions of soil variables for each seedling quadrat. This kriging interpolation was implemented using the gstat package (Pebesma 2004) in R software (v. 3.0.2) (R Development Core Team 2014). The volumetric soil water content (%) was measured in the late dry season of 2013, using the mean values of three replicates taken randomly around the center of each seedling quadrat using a TDR probe (MPM-160B) at a depth of 5 cm (Song et al. 2013).

Topography: The topographic variables used were elevation, convexity, slope and aspect for each seedling quadrat. As above, the full plot was divided into 500 20×20 m subplots with seedling quadrats located at the centers of these subplots. The elevation of each seedling quadrat was taken as the mean of values at each of the four corners of the 20×20 m subplots. The convexity of each seedling quadrat was calculated by subtracting the mean of the four corner elevations of the surrounding 20×20 m subplots from the elevation at its center. The slope was calculated as the mean angular deviation from horizontal of each of the four triangular planes of the 20×20 m subplot formed by connecting three of its corners. Aspect was calculated as below:

$$\text{Aspect}=180-\arctan\left(\frac{fy}{fx}\right)\times\left(\frac{180}{\pi}\right)+90\times\left(\frac{fy}{|fx|}\right)$$

Where *fx* was the elevation difference from east to west in the 20×20 m subplot while *fy* was that from North to South.

To reduce the colinearity of habitat variables in our models, we used a principal components analysis (PCA) in the Vegan package (Dixon 2003) of the R software (v. 3.0.2) (R Development Core Team 2014) on the fourteen habitat variables (soil pH, C, TN, TP, TK, AN, AP, AK, soil bulk density, soil moisture, elevation, slope, aspect and convexity). Canopy openness was not included in the PCA and was inserted into models directly. The first two principal components,

accounting for 56.96% variation of these fourteen habitat variables, were used in the later analysis. The first principal component was associated with high elevation and convexity, and low TN, TP, TK, AN, AP, AK, C, pH and soil moisture. The second principal component was associated with high TN, AN, C, elevation and convexity, and low AK, pH, soil bulk density and soil moisture (Table S2).

Statistical analysis

We conducted analyses separately for all living seedlings in each census interval (2010-2011, 2011-2012, 2012-2013 and 2013-2014). Living seedlings at any one census included survivors from the previous census and new recruits from the most recent census interval.

Generalized linear mixed models (GLMMs) were constructed using the lme4 package (Bates et al. 2014) in R software (v. 3.0.2) (R Development Core Team 2014) to model the probability of seedling survival as a function of explanatory variables, with binomial errors (Bolker et al. 2009). Due to the unknown age of seedlings in this study, we included seedling height as a covariate in our models to account for the fact that larger seedlings have higher survival, and therefore to approximately exclude effects of age on survival. The focal seedling height was log-transformed, and all continuous explanatory variables were standardized by subtracting the mean value of the variable (across all individuals in the analysis) and dividing by 1 standard deviation before analyses. This allowed us to compare directly the relative importance of these explanatory variables (Gelman and Hill 2006). The means and ranges of all continuous explanatory variables used in the analysis are listed in Table S3.

It is possible that spatial autocorrelation exists in seedling survival due to unexplored habitat and other factors. However, previous studies have found that spatial autocorrelation in

269 tropical seedling survival is negligible at distances >5 m (Queenborough et al. 2007), and
270 seedling quadrats in this study were spaced 20 m apart. Therefore, we added random 'seedling
271 quadrat' effects to our models to exclude any effect of spatial autocorrelation within quadrats on
272 our results. Previous studies suggest that this should be sufficient to account for autocorrelation
273 (Comita et al. 2009, Chen et al. 2010). Furthermore, we included species identity as a random
274 effect, because seedlings of different species were expected to respond differently to local
275 neighborhood variables (Lin et al. 2012).

276 In the simplest, density-independent model, seedling survival depended only on the initial
277 heights of focal seedlings (Table 1, Appendix 1). This model was grounded in evidence that the
278 probability of seedling survival increases with increasing seedling stature (Paine et al. 2012).
279 Given the importance of habitat filtering on seedling survival, we then built a habitat-only model,
280 including habitat variables in addition to initial seedling height (Table 1, Appendix 1). To assess
281 the role of neighbor densities on seedling survival, we then built models in which conspecific
282 and heterospecific neighbor effects were included together and separately. In these density-
283 dependent models, seedling survival depended on initial seedling height, the total seedling
284 neighbor density or conspecific and heterospecific seedling neighbor densities, and the total adult
285 neighbor density or conspecific and heterospecific adult neighbor densities (Table 1, Appendix
286 1). To assess the importance of evolutionary relationships in the survival model, we finally
287 constructed phylogenetic density-dependent models in which heterospecific neighbor densities
288 were replaced by the phylogenetic diversity indices described above (Table 1, Appendix 1).

289 Akaike's Information Criterion (AIC) was used to compare models, with ΔAIC calculated
290 by subtracting the overall minimum value of AIC from each of the models' AIC values. We

291 selected the most parsimonious models among those with ⊿AIC less than 2, which are thought to
292 be the equally best-fitting models (Burnham and Anderson 2002). We identified the best-fitting
293 density-dependent model (Table S4) and the best-fitting phylogenetic density-dependent model
294 (Table S5).

295 To explore the influence of habitat filtering on the detection of CNDD and PNDD, we
296 compared the best-fitting density-dependent model to the equivalent model in which habitat
297 variables were included (density + habitat model) (Table 1, Appendix 1). We also compared the
298 best-fitting phylogenetic density-dependent model with its equivalent phylogenetic + habitat
299 model (Table 1, Appendix 1). We also included interactions between habitat variables and
300 neighborhood variables and used AIC scores to identify the best interaction terms combination in
301 both the 'density + habitat' model (Table S6) and the 'phylogenetic + habitat' model (Table S7).
302 In total, we ran six classes of model: (1) density-independent; (2) habitat-only; (3) density-
303 dependent; (4) density + habitat; (5) phylogenetic density-dependent and (6) phylogenetic +
304 habitat. Equations defining these models can be found in Appendix 1.

305 We analyzed the above six model classes for each of the four one-year census intervals
306 (Table 1). To explore the effects of habitat filtering on the detection of CNDD and PNDD, we
307 compared the estimated coefficients of neighborhood variables in four of our models: the best-
308 fitting density-dependent model (model I in Table 2), the density + habitat model with the same
309 neighborhood variables as in the best-fitting density-dependent model (model II in Table 2), the
310 best-fitting phylogenetic density-dependent model (model III in Table 2) and the phylogenetic +
311 habitat model with the same neighborhood variables as in the best-fitting phylogenetic density-
312 dependent model (model IV in Table 2). We labelled models I and II as 'density models', and

313 models III and IV as 'phylogenetic models'. The estimated coefficients represent the relative
314 strength of the variables' effects, and coefficients > 0 indicate positive effects on seedling
315 survival while coefficients < 0 indicate negative effects. Specifically, a positive estimated
316 coefficient for phylogenetic diversity indices indicates a negative relationship between the
317 phylogenetic similarity of heterospecific neighbors and seedling survival (and vice versa). We
318 calculated the variance for each of the models' fixed effects, random effects and for the residuals
319 in each of the above four models (Table S8).

320 To determine whether and how habitat filtering affects the detectability of CNDD and
321 PNDD among species, we added species-specific random slopes for each neighborhood variable
322 in the above four models. Differences between these slopes within a model, and across models
323 with and without habitat variables, were used to capture species-specific responses to neighbor
324 densities and the extent to which habitat filtering might obscure these responses. We used
325 likelihood ratio tests to assess the significance of added species-specific random slopes (Table
326 S9). If *P* values were less than 0.05, we inferred that the coefficients of neighborhood variables
327 did vary across species. We also used two-sample Kolmogorov-Smirnov tests to compare the
328 distributions of the species-specific coefficients of neighborhood variables between the varying-
329 slope models with and without habitat variables.
330
331 **RESULTS**
332 CNDD, PNDD and habitat filtering for seedling survival in the best-fitting model
333 In the 414 target seedling quadrats, there were 8324, 7868, 7680 and 8156 living seedlings of
334 238, 237, 240 and 262 focal woody plant species in the 2010, 2011, 2012 and 2013 censuses
335 respectively.

Of the six survival models we built, the phylogenetic + habitat model had the best-fit for the 2011-2012 and 2013-2014 census intervals, while the density + habitat model and habitat-only model had the best-fit for 2010-2011 and 2012-2013 respectively (Table 1). Across all four census intervals, seedling survival was mainly influenced by fixed effects for habitat variables, followed by the density of conspecific seedling and adult neighbors and NTPd' of heterospecific seedling and adult neighbors (Fig. 1). The effects of the first principal component of topographic and edaphic variables were significantly positively correlated with seedling survival for three census intervals (2010-2011, 2011-2012 and 2013-2014), whereas canopy openness was significantly negatively related for the 2012-2013 census interval. Conspecific adult neighbors had significantly negative effects on survival for the first three census intervals (Table 2). Across all four census intervals, seedling and adult NTPd' generally had insignificant negative effects.

How does habitat filtering affect the detection of CNDD?

Across all four census intervals, the coefficients of conspecific seedling and adult neighbor densities were smaller in Models I and III (without habitat variables) than in Models II and IV (with habitat variables) (Table 2). There were also significant positive interactions between habitat variables and conspecific seedling and adult neighbor densities in Models II and IV (Table 2). Furthermore, we found that adding habitat variables increased the variance explained by the densities of conspecific seedling and adult neighbors, while variances explained by random effects remained almost constant (Table S8). Together, these results indicate that the true extent of CNDD was obscured when not accounting for habitat variables.

Because adult CNDD was significant in the best-fit models for 2010-2011 and 2011-2012 (Table 2), we added species-specific random slopes for conspecific adult neighbor density to

these models. The distribution of these species-specific coefficients changed significantly between models with and without habitat variables (Models II and IV vs. I and III; two-sample Kolmogorov-Smirnov test, $p < 0.05$, Fig. 2). When taking into account habitat variables in Model II, we found that 97.90% and 97.47% of the focal species in the 2010-2011 and 2011-2012 census intervals suffered stronger negative effects of conspecific adult neighbor densities than those in equivalent non-habitat informed models (Model I). Similarly, 98.32% and 92.83% of the focal species in Model IV (with habitat variables) suffered stronger negative effects than those in model III (without habitat variables).

How does habitat filtering affect the detection of PNDD?

Across all four census intervals, the coefficients of seedling NTPd' and adult NTPd' were generally negative in both Models III (without habitat variables) and IV (with habitat variables) (Table 2), indicating that seedlings survived significantly better when growing among closely related heterospecific neighbors. In contrast to conspecific neighbor densities, adding habitat variables into the survival models did not substantially affect the coefficients of the phylogenetic diversity indices, and the interactions between habitat variables and s_NTPd' and a_NTPd' were insignificant (Table 2). The inclusion of species-specific random slopes for seedling NTPd' and adult NTPd' did not significantly increase the variation explained (Table S9). Thus, we did not conduct further analyses into how habitat filtering affected the variation of PNDD among species.

DISCUSSION

Conspecific negative density dependence (CNDD), phylogenetic negative density dependence

(PNDD) and habitat filtering are often cited as prominent mechanisms maintaining the composition and diversity of communities. Some studies have discussed a potentially confounding influence of habitat filtering when attempting to quantify negative density dependence (Comita et al. 2009, Chen et al. 2010, Bai et al. 2012, Piao et al. 2013), but this has not previously been well documented. Our results show that CNDD and habitat filtering simultaneously influence seedling survival. Taking habitat variables into account elucidated more clearly the negative impacts of conspecific neighbors (seedlings + adults) on seedling survival, and made the species-specific negative effects of conspecific neighbor densities generally stronger. Our study system showed the opposite effect with respect to PNDD. In the following we discuss these results in more detail.

Local neighborhood and habitat effects

Seedling-seedling and seedling-adult interactions may be stronger in tropical forests than in subtropical forests (e.g., Chen et al. 2010) or temperate forests (e.g., Bai et al. 2012). We found these interactions, at the scales we considered, were a significant driver of seedling survival. These results are in line with evidence from other tropical forests (e.g., Queenborough et al. 2007, Comita et al. 2009, 2010, Metz et al. 2010, Kobe and Vriesendorp 2011, Johnson et al. 2012, Lebrija-Trejos et al. 2014). The negative effects of conspecific neighbors on seedling survival are consistent with intraspecific competition and the Janzen-Connell hypothesis (Janzen 1970, Connell 1971). Our results show that seedling survival was significantly influenced by densities of conspecific seedling and adult neighbors, which may be involved in intraspecific competition for shared resources and/or as a source for specialized natural enemies (herbivore and pathogen) (e.g., Augspurger 1984, Packer and Clay 2000, 2003, Bell et al. 2006, Freckleton

and Lewis 2006, McCarthy-Neumann and Kobe 2008). Another possible explanation for the negative impact of conspecific adult neighbors is that their presence implies that there may be many more conspecific seedling neighbors over the wider area (beyond our seedling quadrats), making competition and mortality due to pests and pathogens even greater than we expect from measured seedling densities.

Recently, several studies focusing on NDD for seedling survival have scaled the effects of heterospecific neighbors by phylogenetic relatedness. For example, Liu et al. (2012) found a phylogenetic Janzen-Connell effect, which might be caused by associated host-specific fungal pathogens in a subtropical forest. Metz et al. (2010) found that seedling survival increased where nearby adult neighbors were more distantly related to focal seedlings. The critical factors affecting a pathogen's infection of a host plant are morphological and biochemical, which are often phylogenetically conserved (Mitter et al. 1991). Further, empirical evidence has shown that closely related species are more likely to share the same or similar pests and pathogens (e.g., Novotny et al. 2006, Gilbert and Webb 2007, Gilbert et al. 2012, Liu et al. 2012), and to have several similar key functional traits (Yang et al. 2014). Thus, the effects of neighbors on a focal plant should depend upon phylogenetic similarities, and should be less negative for less related plants. However, we found a negative effect of phylogenetic diversity, indicating that increased phylogenetic similarities between heterospecific neighbors and focal seedlings increased seedling survival. Our results therefore do not support PNDD. While these findings are in contrast to those of the studies cited above, they are consistent with several other studies that have shown that plants perform better when heterospecific neighbors are relatively closely related (summarized in Lebrija-Trejos et al. 2014). Our results also suggest that this phylogenetic positive density-dependence (PPDD) is a more important determinant of seedling survival than

PNDD (see below).

The edaphic and topographic variables in our study had important effects on seedling survival. Specifically, the positive effect of the first principal component of edaphic and topographic variables on seedling survival demonstrated that the availability of below-ground resources is also an important driver of tree seedling survival (Comita et al. 2009, Bai et al. 2012, Piao et al. 2013). Many works have also shown that light availability has a strong effect on the performance of shade-tolerant seedlings in tropical forests (e.g., Paz and MartÍnez-Ramos 2003, Comita et al. 2009, Queenborough et al. 2009). However, light availability had a slight negative effect on seedling survival in our study, even though the range of canopy openness we found was sufficient to produce positive effects (with approximately 90% of seedling quadrats within a range of canopy openness between 0.29% and 3%). This unexpected relationship may indicate a widespread problem with the use of canopy photographs in studies of this kind (e.g., Comita et al. 2009; Lin et al. 2014).

Habitat filtering and CNDD

The increase in survival driven by favorable habitat may offset the thinning of conspecific trees due to CNDD (Wright 2002). A positive relationship with conspecific densities would therefore be found when host-specific natural enemies or intra-specific competition do not offset the advantages of occurring in a preferred habitat (at least until the population size becomes too large). A few studies have shown such an interaction between habitat variables and negative density dependence. For example, Piao et al. (2013) suggested that a failure to take into account the confounding effect of habitat heterogeneity may lead to mischaracterization of the role of density dependence in shaping plant communities. Zhu et al. (2010) found that factoring out

habitat heterogeneity made most tree species show negative density dependence in a subtropical forest, but did not explore in detail exactly how habitat variables affected density dependence.

Our work clearly shows that taking habitat variables into consideration made the effects of conspecific neighbors appear more negative in both the density models and the phylogenetic models (Table 2). The significant positive interactions between habitat variables and conspecific seedling and adult neighbor densities (Table 2) implied changes in CNDD across different habitat conditions. This is why the variance explained by the densities of conspecific seedling and adult neighbors increased in models with habitat variables (Table S8).

The impact of habitat filtering on the detection of CNDD can also be seen in the prevalence of species-habitat associations at both seedling and adult stages in the XSBN plot (Table S10). Of the species with more than 20 surveyed seedlings, 41.77% and 60.76% showed significant habitat preferences at the seedling stage and the adult stage, respectively. Our results therefore suggest that conspecific negative density dependence is evident at lower densities in marginal habitats and only at higher densities in optimal habitats. Further, the inclusion of habitat variables led to an increase in apparent strength of species-specific negative effects of conspecific neighbors, especially conspecific adult neighbors. In sum, CNDD and habitat filtering both had vital influences on seedling dynamics and the observed effects of conspecific neighbors were the result of an interaction between them.

Lack of evidence for PNDD

Though more and more ecologists have concluded that phylogenetic density dependence is an important mechanism for seedling dynamics and coexistence (e.g., Webb et al. 2006, Metz et al. 2010, Zhu et al. 2015), the influence of habitat filtering on the detection of phylogenetic density dependence had not been taken into account. As with conspecifics, the impact of natural enemies

and the stronger competition for similar resources among closely related neighboring plants should lead to a negative effect of phylogenetic similarity on seedling survival. An apparently positive relationship between phylogenetic similarity and seedling survival might be caused by habitat filtering, because closely related plants may often have similar habitat requirements (Vamosi et al. 2009, Baldeck et al. 2013). We expected that habitat filtering could therefore affect the detection of the negative effect of phylogenetic similarity on seedling survival in the same way that it affected CNDD detectability. However, this expectation was not met in this study. While we did find that the inclusion of phylogenetic relatedness of heterospecific neighbors improved model accuracy, we found no evidence of PNDD. Furthermore, differences in the effects of phylogenetic relatedness between survival models without and with habitat variables were relatively slight. Instead, we found evidence of phylogenetic positive density-dependence (PPDD). There appears to be an emerging consensus about the existence of this effect, perhaps due to the shared habitat preferences between closely related individuals (Lebrija-Trejos et al. 2014). However, our results showed that seedling survival was greater among closely related heterospecific neighbors even when habitat variation was controlled (Model IV in Table 2). While it is possible that unobserved habitat factors had a confounding effect on this analysis, it is not clear what these factors might be, and it seems unlikely that they could be strong enough to reverse the apparent direction of relationships between seedling survival and neighbor relatedness. We therefore suggest that PPDD, as detected here, may be a real and independent effect of some as-yet unrecognized mechanism.

CONCLUSIONS

To the best of our knowledge, our study is the first to explore the joint effects of conspecific

497 negative density-dependence (CNDD), phylogenetic negative density-dependence (PNDD) and
498 habitat filtering and their relative importance for tropical tree seedling survival. Our results
499 demonstrate that replacing heterospecific neighbor densities with phylogenentic diversity indices
500 improved survival models, which is in line with an increasing awareness of the importance of
501 evolutionary relationships in neighborhood dynamics. However, the effect of phylogenetic
502 diversity indices in our study system was opposite to that expected under PNDD, even when we
503 controlled for the effects of habitat. CNDD and habitat filtering played important roles in
504 seedling survival simultaneously. The observed effect of conspecific neighbor densities is
505 primarily a result of an interaction between habitat filtering and conspecific neighbor densities,
506 making CNDD detectable at lower densities in marginal habitats than in preferred habitats.
507 Therefore, adding habitat variables into survival models strengthens the measured negative
508 effects of conspecific neighbors on seedling survival. We conclude that future studies of
509 neighborhood density dependence must take habitat filtering and phylogenetic relationships into
510 account in order to properly assess the effects of conspecific and heterospecific neighbors, and
511 the occurrence and cause of phylogenetic positive density-dependence.

ACKNOWLEDGEMENTS

This study was supported by National Key Basic Research Program of China (Grant No. 2014CB954104), the National Natural Science Foundation of China (31370445), the West Light Foundation of Chinese Academy of Sciences and the Applied Fundamental Research Foundation of Yunnan Province (2014GA003). NGS was funded by NSF Dimensions of Biodiversity US-China grants (DEB-1241136; DEB-1046113). We thank David L. Erickson and W. John Kress for their assistances on the construction of molecular phylogenetic tree, Lang Ma, Yongzhen Shen, Jiu Ma, Zhenhua Sun, Shishun Zhou, Wenfu Zhang, Xiaofei Yang and Xiaobao Deng for their assistances in seedling censuses and species identification. Special thanks to all the people who have contributed to the establishment of the 20-ha Xishuangbanna tropical seasonal rain forest dynamics plot. Logistical support was provided by Xishuangbanna Station of Tropical Rainforest Ecosystem Studies (National Forest Ecosystem Research Station at Xishuangbanna), Chinese Academy of Sciences. We thank S. Joseph Wright and one anonymous reviewer for their critical comments on the manuscript.

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709 TABLES

710 TABLE 1. AIC values for the six classes of model for each of the four one-year census intervals.

Candidate model	AIC			
	2010-2011	2011-2012	2012-2013	2013-2014
Density-independent model				
H	3463.1	3213.7	4227.3	4997.7
Habitat-only model				
H+ light+ PCA1+ PCA2	3448.3	3203.9	**4225.2**	4998.8
Density-dependent model[†]				
H + cons+hets +CA+ HA	3462.6	3214.8	4230.2	5003.1
Density +habitat model[††]				
H + cons+hets +CA+ HA +light+ PCA1+ PCA2+cons×PCA1+ cons×PCA2+CA×PCA1+ CA×PCA2	**3442.0**	3201.9	4234.0	4998.2
Phylogenetic density-dependent model[‡]				
H +cons+ s_NTPd'+CA+a_ NTPd'	3466.0	3211.4	4230.1	5000.4
Phylogenetic +habitat model[§]				

H +cons+ s_ NTPd'+CA+a_ NTPd'+light + PCA1+ PCA2+ cons×PCA1+cons×PCA2+ CA×PCA1+ CA×PCA2+s_ NTPd' ×PCA1+ s_ NTPd' ×PCA2+ a_ NTPd' ×PCA1+ a_ NTPd' ×PCA2	3449.1	**3196.9**	4234.7	**4996.6**

711 †The model comparison for density-dependent models is shown in Table S4. ††The model
712 comparison for density + habitat models with different interaction term combinations is shown in
713 Table S6. ‡The model comparison for phylogenetic density-dependent models is shown in Table
714 S5. §The model comparison for phylogenetic+habitat models with different interaction
715 combinations is shown in Table S7. 'H' is the heights of focal seedlings. Neighborhood variables
716 included the density of conspecific seedling neighbors (cons), the density of heterospecific
717 seedling neighbors (hets), sum of conspecific adults' basal areas weighted by the distance
718 between the focal seedling and the adult neighbors at distances up to 20 m (CA), sum of
719 heterospecific adults' basal areas weighted by the distance between the focal seedling and the
720 adult neighbors at distances up to 20 m (HA), and two phylogenetic diversity indices: relative
721 nearest taxon phylogenetic diversity between heterospecific seedling neighbors and focal
722 seedlings (s_NTPd') and relative nearest taxon phylogenetic diversity between heterospecific
723 adult neighbors and focal seedlings (a_NTPd'). Habitat variables included canopy openness %
724 (light) and the first two principal components (PCA1and PCA2) of soil properties and
725 topography. ΔAIC is calculated by subtracting the minimum AIC value from each of AIC values
726 of the models. We selected the most parsimonious models among the models with $\Delta\text{AIC} \leq 2$
727 (AIC in bold) (Table S2).

728 TABLE 2. Coefficient estimates for all explanatory variables in the density-dependent model (Model I), the density + habitat model
729 with the same neighborhood variables as that in the density-dependent model (Model II), the phylogenetic density-dependent model
730 (Model III) and the phylogenetic + habitat model with the same neighborhood variables as that in the phylogenetic density-dependent
731 model (Model IV), for each of the four one-year census intervals.

Explanatory variables	2010-2011				2011-2012				2012-2013				2013-2014			
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Intercept	3.686***	3.640***	3.663***	3.601***	3.616***	3.581***	3.584***	3.514***	2.849***	2.830***	2.827***	2.811***	2.691***	2.633***	2.644***	2.599***
Height	0.698***	0.678***	0.696***	0.678***	0.783***	0.779***	0.783***	0.748***	0.323***	0.318***	0.322***	0.314***	-0.037NS	-0.037NS	-0.037NS	-0.038NS
cons	0.095NS	0.006NS	0.042NS	-0.019NS	0.076NS	-0.038NS	0.075NS	-0.022NS	0.071NS	0.042NS	0.052NS	0.034NS	-0.010NS	-0.115NS	-0.029NS	-0.125NS
hets	0.159NS	0.088NS			0.002NS	-0.059NS			0.054NS	0.050NS			0.047NS	0.026NS		
CA	-0.110*	-0.169**	-0.116*	-0.187**	-0.127*	-0.166**	-0.125*	-0.185**	-0.091*	-0.113NS	-0.090*	-0.117*	-0.055NS	-0.095NS	-0.052NS	-0.093NS
HA	0.002NS	0.035NS			0.003NS	0.020NS			-0.026NS	-0.010NS			-0.061NS	-0.045NS		
s_NTPd’			-0.029NS	-0.025NS			-0.100NS	-0.137*			-0.016NS	-0.055NS			-0.016NS	-0.024NS
a_ NTPd’			-0.034NS	0.001NS			-0.083NS	-0.028NS			-0.071NS	-0.059NS			-0.157NS	-0.140NS

light	-0.084NS	-0.076NS	-0.025NS	-0.020NS	-0.177**	-0.170*	-0.059NS	-0.065NS
PCA1	0.328***	0.314***	0.299***	0.272***	0.117NS	0.106NS	0.197**	0.201**
PCA2	0.261**	0.245**	0.202**	0.143NS	0.103NS	0.106NS	0.025NS	0.038NS
cons×PCA1	0.103NS	0.084NS	0.056NS	0.053NS	0.069NS	0.056NS	0.118NS	0.121NS
cons×PCA2	0.029NS	0.011NS	0.167*	0.138NS	-0.001NS	-0.015NS	0.004NS	0.011NS
CA×PCA1	0.150*	0.133NS	0.072NS	0.088NS	0.041NS	0.035NS	0.164**	0.165**
CA×PCA2	0.224**	0.212**	0.052NS	0.055NS	0.021NS	0.022NS	0.089NS	0.083NS
s_NTPd'×PCA1		0.059NS		0.032NS		0.020NS		-0.082NS
s_NTPd'×PCA2		0.016NS		0.128*		0.115*		0.063NS
a_NTPd'×PCA1		0.017NS		0.073NS		0.044NS		0.011NS
a_NTPd'×PCA2		0.051NS		0.093NS		-0.041NS		-0.086NS

732 * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant. See Table 1 for variable abbreviations.

733

734 Figure Legends

735

736 FIG. 1. Estimated effects (± 2SE) of neighborhood variables and habitat variables on seedling
737 survival for each of the four one-year census intervals in phylogenetic + habitat model (Model IV
738 in Table 2). Filled circles indicate significant effects ($P < 0.05$). The interactions of neighborhood
739 variables and habitat variables were not shown here and can be found in Table 2. See Table 1 for
740 variable abbreviations.

741

742 FIG. 2. A comparison of the frequency distribution of species-specific coefficients of conspecific
743 adult neighbor density between model I (Density model without habitat variables) and model II
744 (Density model with habitat variables), and between model III (Phylogenetic model without
745 habitat variables) and model IV (Phylogenetic model with habitat variables) for 2010-2011 and
746 2011-2012 census intervals. Bars to the left of the dashed zero line indicate species whose survival
747 is reduced by increasing neighborhood variables.

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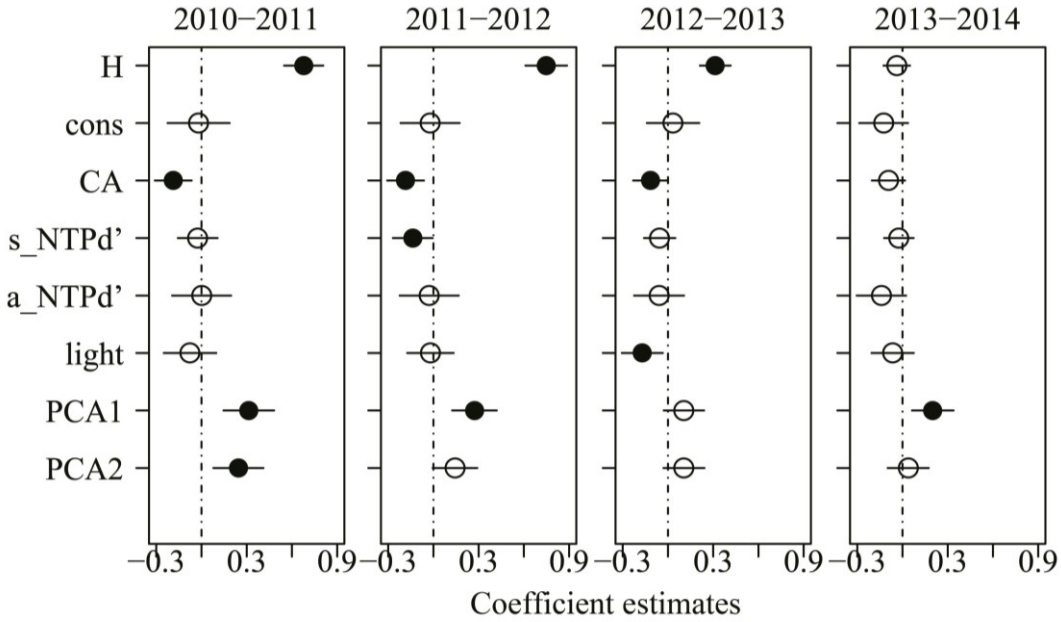
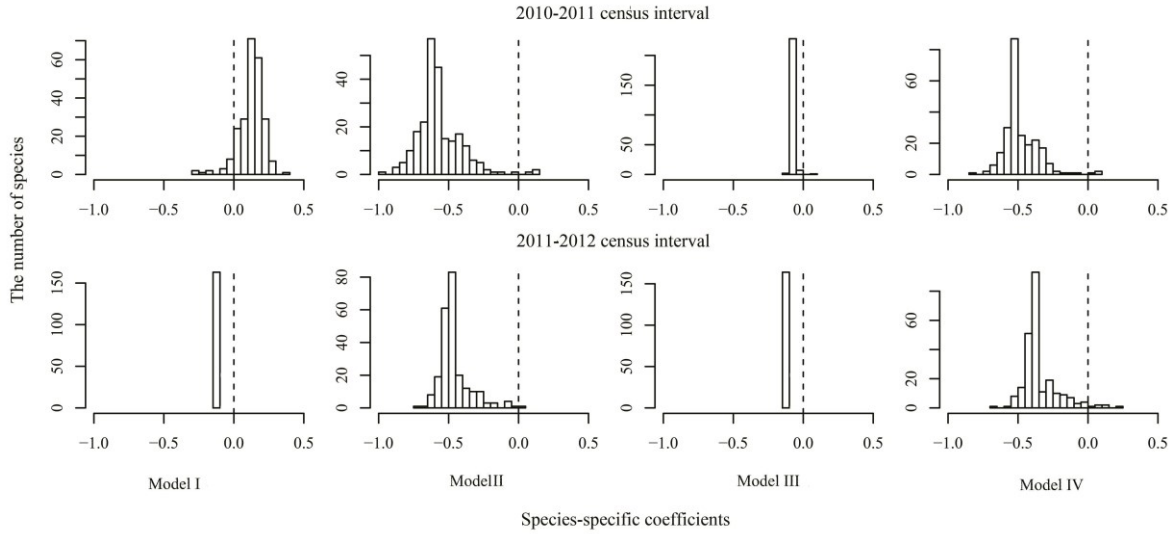
750


2010−2011
2011−2012
2012−2013
2013−2014
H
cons
CA
s_NTPd'
a_NTPd'
light
PCA1
PCA2
−0.3
0.3
0.9
Coefficient estimates

751

752


2010-2011 census interval
2011-2012 census interval
The number of species
Model I
ModelII
Model III
Model IV
Species-specific coefficients

753